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GAMETOGENESIS AND LARVAL PRODUCTION IN A POPULATION OF THE INTRODUCED ASIATIC CLAM, *CORBICULA* SP. (BIVALVIA:CORBICULIDAE), IN MARYLAND

VICTOR S. KENNEDY AND LAURIE VAN HUEKELEM

Horn Point Environmental Laboratories, University of Maryland, Box 775, Cambridge, Maryland 21613

Abstract

Histological assessment of gametogenesis and larval production in monthly samples of *Corbicula* sp. collected from December 1981 to October 1983 in the Potomac River, Maryland, revealed that the clams were simultaneous hermaphrodites. Gametes of both sexes were present year-round, including winter, although male reproductive tissue was less common than female tissue. Both male and female tissue were found in the smallest clam examined (9.6 mm long). Eggs and sperm were often produced in the same follicle and occurred together in the gonoducts of a number of specimens. Stereological analysis was used to quantify tissue change during the study. No clear cycles of reproductive tissue volume fractions (developing or ripe gametes) were demonstrated, suggesting that this species may be capable of responding rapidly throughout the year to suitable environmental conditions by spawning. In our samples, larvae were produced over two extended time periods, one in spring and one in fall, with the months involved varying somewhat from year to year. The smallest clam containing larvae was 13.4 mm long.

Introduction

Asiatic clams of the genus *Corbicula* were apparently introduced to the West Coast of North America prior to 1938 and their descendants have since become widespread in fresh waters of the continent (Britton and Morton, 1982; McMahon, 1982). In some areas they have become so abundant that they foul irrigation canals and industrial plumbing systems, including the water-supply systems of electric power plants (McMahon, 1977; Mattice, 1979), to the point of becoming pests of commercial significance.

In Maryland, Stotts *et al.* (1977) were the first to report on the presence of Asiatic clams, in this case at the mouth of the Susquehanna River. Dresler and Cory (1980) reported that *Corbicula fluminea* had become established in the Potomac River on the Western Shore of Chesapeake Bay, and Counts (1981) recorded this species from the Wicomico River on the Eastern Shore. Since then, we have collected Asiatic clams from Nassawango Creek, which is a tributary of the Pocomoke River in Maryland, and from Butler Mill Creek which flows into Lewis Creek, a short tributary of the Nanticoke River just across the Maryland state line in Delaware.

With these clams thus becoming widely distributed in Maryland and adjacent waters in recent years, we embarked on a study of reproduction in a large population living in the Potomac River. There have been some studies of Asiatic clam reproduction elsewhere in North America, predominantly in the South (see Britton and Morton, 1982 and McMahon, 1983 for reviews) but none reported for the Mid-Atlantic states

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or for natural waters (*i.e.*, not industrially heated) this far north. None of the studies used quantitative evaluation of gametogenesis. We employed a recently described quantitative method of stereological analysis (Lowe *et al.*, 1982) to delineate gametogenic patterns in our study population, and we also documented periods of larval production.

Taxonomic status of Asiatic clams

With regard to the species of Asiatic clam we studied, Britton and Morton (1979) declared that *Corbicula fluminea* was the correct scientific name of North American animals. However, Hillis and Patton (1982) presented electrophoretic evidence that two "species" of *Corbicula* (one with white nacre and one with purple nacre) live in the Brazos River, Texas. We have also found a clam population with purple nacre in Butler Mill Creek, although all other populations in the Bay watershed that we have examined (four) have white nacre. While the Maryland clams studied for this report are similar to those being called *Corbicula fluminea* (white form), we feel that assignment of a species name is not warranted until conclusive taxonomic studies have been performed. We therefore refer to our research animals as *Corbicula sp.* When referring to the reported works of others, we have retained the species' names they used. Voucher specimens of our Whites Ferry study population (USNM 804414) and the Butler Mill Creek population (USNM 836237) have been deposited with the Smithsonian Institution's National Museum of Natural History.

Materials and Methods

With the aid of a mesh-lined clam rake, Asiatic clams were collected at approximately monthly intervals (except when the river was frozen or during high river flow periods) from shallow inshore water just below Whites Ferry, Maryland (approx. 39°09′ N; 77°31′ W), on the Potomac River. Collections began in December 1981 and ended in October 1983. Temperatures were measured at time of collection.

Except for early samples, two sets of about 20 animals each were selected to cover a range of lengths (measured to the nearest millimeter along the anterior-posterior axis). These clams were held in reverse-osmosis water for 1–2 days to allow them to cleanse themselves of dirt. They were then shucked whole. Individual dry body tissue weights for one set of clams (size range: 7.5–33.5 mm) were determined by holding the shucked clams at 95°C for 24 h and then weighing them to provide data for log length *versus* log dry weight analysis using least-squares regression. The second set of clams [size range: 9.6–41.9 mm (Table I), with 65% in the 20–30 mm range] was fixed for 24 h in Davidson's Solution at 4 to 8°C, placed in 50% alcohol for at least 2 h at room temperature, and stored in 70% alcohol. Fixed clams were taken through an ascending alcohol series, cleared in xylene, and embedded in 56°C Paraplast. Sections were cut at 6–8 μm thickness and stained in Harris' hematoxylin and counterstained in eosin.

To determine the best orientation for viewing reproductive follicles in body tissue and to ensure that we obtained the most representative section of the tissue, we initially prepared both transverse (cross) and sagittal (longitudinal) sections. We concluded that sagittal sections were more satisfactory for viewing a wider area of gill and body tissue and these sections were thus used exclusively in this study. In preparing sections, when the first section containing substantial follicular tissue was encountered it was retained and two to four additional body sections were cut at 100 μm to 200 μm intervals into the body (depending on clam size). Each of the three to five resulting sections was placed on separate slides for analysis. The sections prepared for each

monthly sample were examined for the presence of larvae in the gills and of eggs and sperm in follicular tissue.

To quantify the process of gametogenesis, stereological analysis (Lowe *et al.*, 1982; Newell *et al.*, 1982) was performed on 10 clams per month (except December 1981 when only 6 were used). A projection microscope was used to project the image of the gonadal tissue in three different sagittal sections per clam onto a sheet of paper marked with 42 points. The coincidence of a point with one of six tissue types, *i.e.*, (1) interfollicular connective tissue; developing (2) male or (3) female gametes; morphologically ripe (4) male or (5) female gametes; and (6) spawning/spent tissue (Fig. 1) was recorded for three randomly selected fields per sagittal section. This provided 9 sets (three fields × three sagittal sections) of 42 determinations of the frequency of occurrence of the 6 tissue components within the gonadal region of each specimen. The average value for each set of nine was calculated for each tissue component, resulting in six average values of tissue frequency for each clam. From these values the percentage volume fraction of each of the six tissue types was determined for each clam (Lowe *et al.*, 1982). Following this, an average volume fraction (%) for each tissue type was calculated for each monthly sample of clams. To calculate confidence intervals, these monthly averages were transformed by arcsine transformation (Sokal and Rohlf, 1981) and are presented retransformed with 95% confidence intervals in Figure 2.

During those periods that larvae were being brooded internally, release of brooded material from animals recently collected in the field would take place in holding bowls. In June 1982, this material was examined and length measurements were made on its components (cleavage stages, trochophores, straight-hinge larvae, juveniles).

Results

Figure 1 presents representative examples of various gametogenic stages, including developing and ripe male and female gametes, spent follicles, and interfollicular connective tissue. The pattern of gametogenesis for Whites Ferry clams is shown in Figure 2 by changes in volume fraction (VF) percentages of six tissue components over time. The preponderant tissue type was interfollicular connective tissue (ICT), the average proportions of which ranged from 74% in August 1982 to 47% in May 1983 and back to 74% in October 1983. Average VF of developing female gametes ranged from 6 to 13% over time; these values were higher than those of contemporaneously developing male gametes (0–6%). Ripe female gametes comprised the second most abundant tissue type (after ICT), ranging from 11 to 28% of all tissues, compared with a range of 0 to 2% for ripe male gametes (the least common tissue type). Finally, spawned or spent tissue ranged in occurrence from 1 to 11% of total tissues examined.

No clear cycles in VF in any of the tissue types are apparent. A peak in proportion of ICT occurred in August 1982 followed by a decline to May 1983 (to a lower point than the previous May). A relatively rapid increase in VF occurred in June and July 1983. Values then declined in August but increased in the following two months. Developing female gametes generally remained within a few percentage points of 10% VF through the sampling period whereas ripe female gametes varied around 20% VF (with a slight tendency for peaks to occur in spring and fall). Both developing and ripe male gametes were very low in VF, with a peak in November 1982 and May–June 1983 for developing male gametes and small peaks in May and September 1982 and June 1983 for ripe male gametes. Spawning or spent tissue was usually less than 10% VF during the year, with peaks in March and June 1982 and May and August 1983.

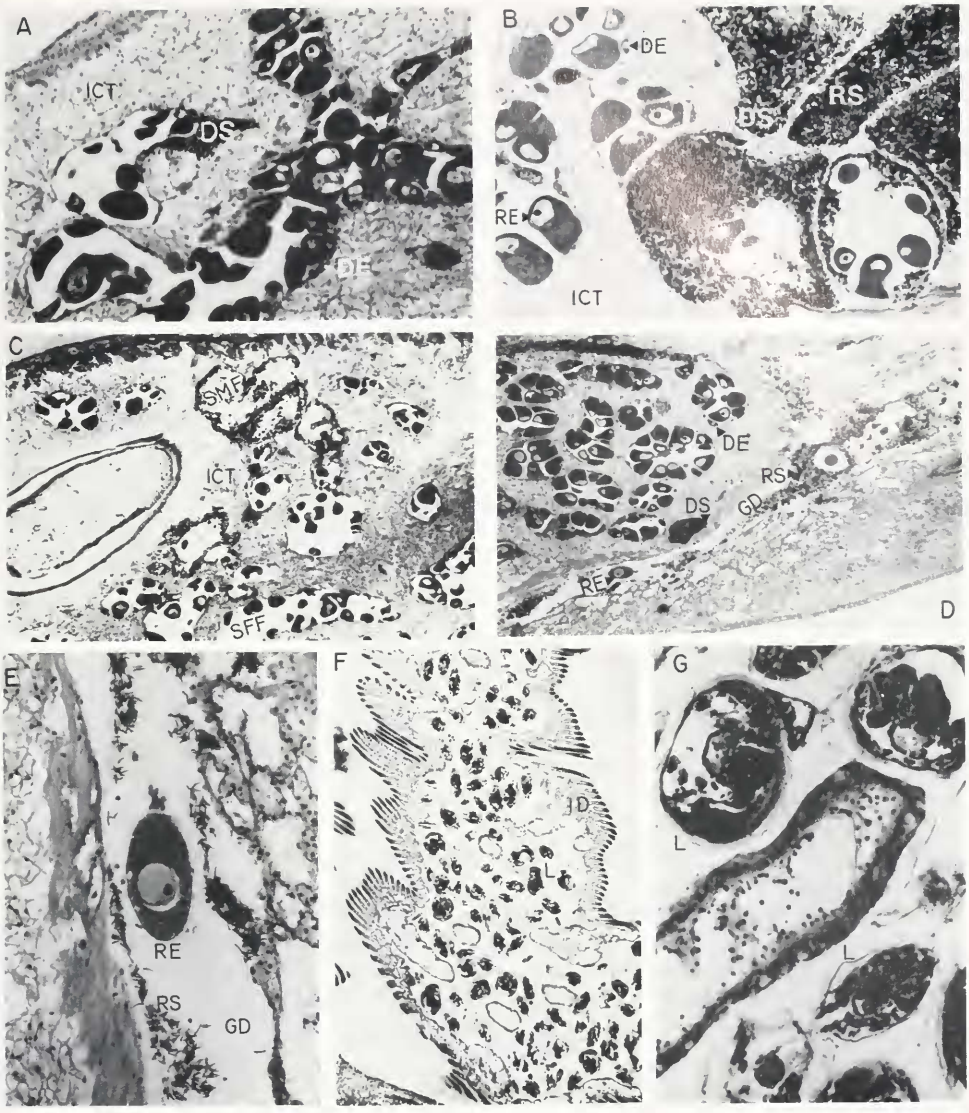

FIGURE 1. Representative examples of gamete development, spawning, gamete intermingling, and larval stages of *Corbicula* sp. A. Follicles containing developing sperm, and developing and ripe eggs; B. As A, later in development, with eggs and sperm co-occurring in some follicles; C. Gonad in advanced spawning/spent state; D. Gonoduct with ripe eggs and ripe sperm intermingling; E. Close-up of D, with egg surrounded by sperm; F. Inner demibranch of gills filled with developing larvae; G. Close-up of larvae in gill. Abbreviations: DE = developing egg; DS = developing sperm; GD = gonoduct; ICT = interfollicular connective tissue; ID = inner demibranch; RE = ripe egg; RS = ripe sperm; SFF = spent female follicle; SMF = spent male follicle. Magnification: 40× = C, D, F; 100× = A, B; 400× = E, G.

Table I lists the percentages of Asiatic clams examined that contained female gametes, male gametes, and larvae. Throughout the study, every clam examined contained female gametes (in October 1983 one clam contained extensive male follicles with almost no eggs present). However, the proportion of clams in which male gametes

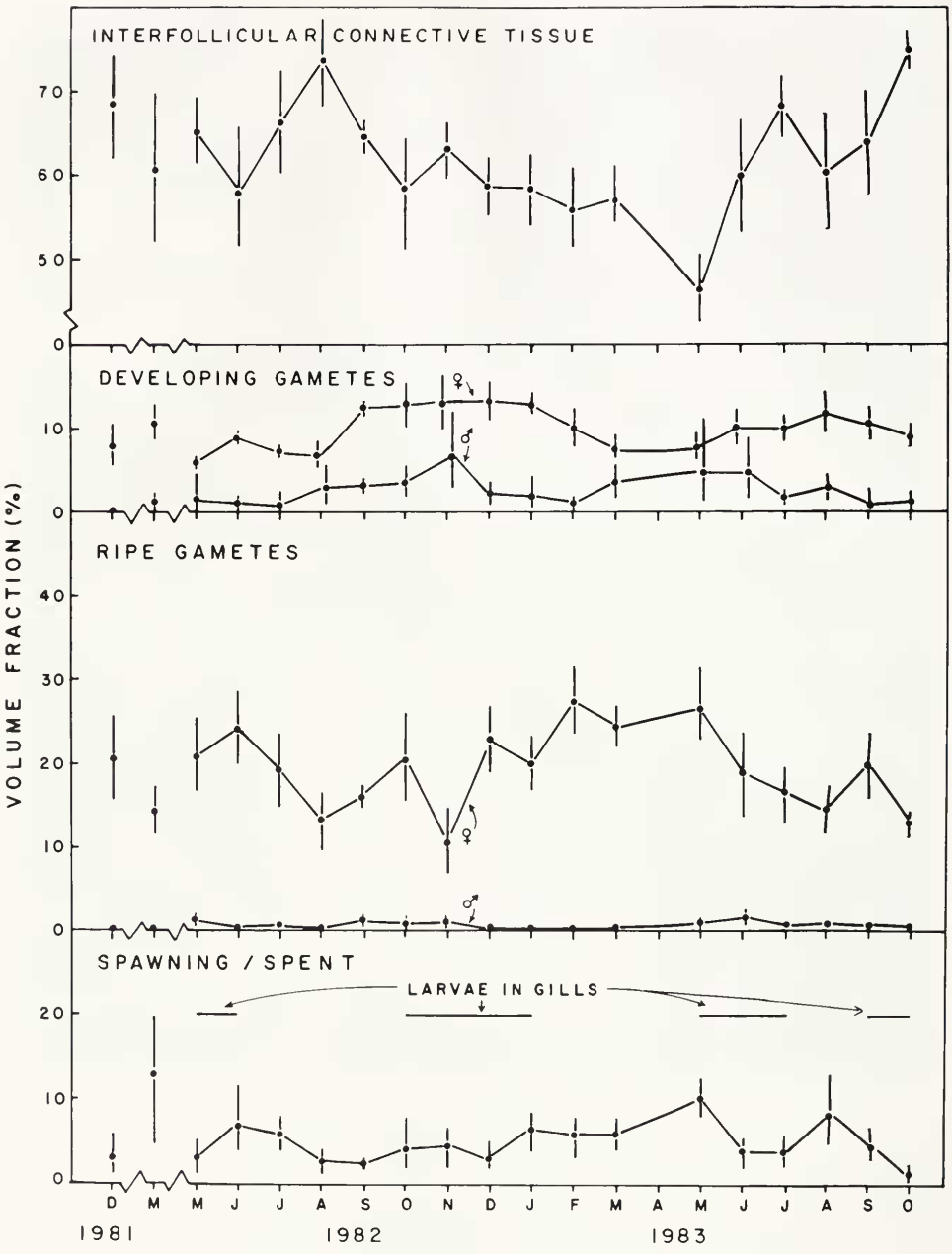

FIGURE 2. Average volume fractions (with 95% confidence intervals) of six tissue components in the gonadal region of *Corbicula* sp. from Whites Ferry, MD.

were noted fluctuated from 43 to 100%, although after March 1982, 85% or more of the monthly samples of clams contained male gametes. The smallest clam we sectioned (9.6 mm) contained both male and female gametes. However, when the

TABLE I

Percentages of Asiatic clams that contained female gametes, male gametes, and larvae (Whites Ferry, Maryland)

Month	Length range (mm)	Female	Male	Larvae
1981 Dec	15.8–24.8	100 (28)[1]	43 (28)	0 (21)
1982 March	18.3–41.9	100 (12)	50 (12)	0 (12)
May	15.6–28.3	100 (16)	88 (16)	67 (15)
June	13.4–23.7	100 (20)	100 (20)	85 (20)
July	14.4–34.7	100 (20)	85 (20)	0 (20)
Aug	18.7–28.9	100 (20)	95 (20)	0 (20)
Sept	21.6–28.1	100 (20)	100 (20)	0 (20)
Oct	13.9–29.0	100 (19)	89 (19)	11 (18)
Nov	9.6–29.0	100 (20)	90 (20)	40 (20)
Dec	11.9–29.2	100 (20)	100 (20)	40 (20)
1983 Jan	19.2–30.1	100 (20)	90 (20)	10 (20)
Feb	23.3–28.8	100 (20)	85 (20)	0 (20)
March	11.6–30.4	100 (20)	100 (20)	0 (19)
May	19.0–29.7	100 (20)	100 (19)	25 (20)
June	21.6–30.9	100 (14)	93 (14)	100 (14)
July	13.1–32.3	100 (20)	90 (20)	45 (20)
Aug	16.7–36.7	100 (20)	90 (20)	0 (20)
Sept	19.8–32.8	100 (20)	95 (20)	80 (20)
Oct	29.7–33.4	100 (20)[3]	90 (20)	75 (20)
Smallest[2]		9.6 mm	9.6 mm	13.4 mm

[1] Number in parentheses is sample size.
[2] Sizes of the smallest animals containing gametes or larvae.
[3] Almost no eggs noted in one animal in which male follicles were widespread.

proportion of clams ≥ 20 mm long with male gametes was compared with clams < 20 mm long with male gametes, the former comprised 92% compared with 78% for the latter size class (this difference is significant at the $P < 0.001$ level as determined by the G-test of independence; Sokal and Rohlf, 1981).

In numerous instances, both male and female gametes were found to be developing within the same follicles (*e.g.*, Fig. 1B). In addition, it was not uncommon during months of spawning to find male and female gametes mingling in gonoducts (*e.g.*, Figs. 1D, E).

Larvae appeared in the inner demibranchs of clams in spring and fall 1982 and in spring–early summer and fall 1983. The smallest clam which contained larvae was 13.4 cm long.

Figure 3 presents information on clam dry weight changes over the study period. Each point represents the predicted dry tissue weight of a representative 20 mm clam as determined from length-weight curves (GM regression; Ricker, 1973) we developed each month (Table II). Coefficients of determination were high and the variance ratios (F_s) for each regression were all significant at $P < 0.001$ (Sokal and Rohlf, 1981). Initially, in December 1981 and March 1982, the predicted dry weight was low (Table II, Fig. 3). It rapidly increased to a peak in May 1982, declined in June, and then increased and reached its highest value for this study in August. Thereafter there was a decline to October 1982 followed by a general increase until January 1983. A decline in February was followed by another peak in March 1983. (Note that the values for December 1982 and March 1983 were higher than they had been

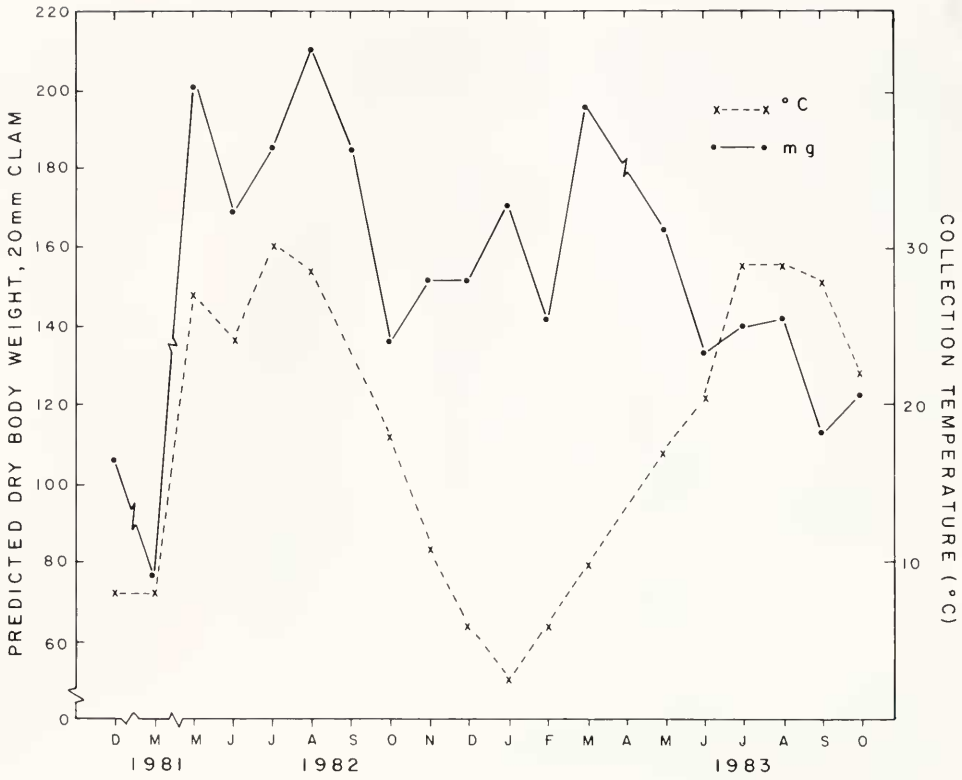

FIGURE 3. Collection temperature and changes in predicted body weight of a representative 20 mm specimen of *Corbicula* sp. from Whites Ferry, MD.

one year earlier.) After March, dry weight declined through June, rose slightly in July and August, then declined again.

Observations of larvae released into bowls by animals recently collected in the field revealed that two kinds of release appeared to occur. In some instances, fully developed juveniles with an active foot were ejected from the adult clam. In other instances, a mixture of material was released; it included juvenile clams, a few younger straight hinge or trochophore larvae, larvae with apical flagellae, and large, ciliated objects that we assume were early cleavage stages or morulae. Samples of this material were measured with an ocular micrometer. The large cilated objects ranged in size from 160 to 220 μm ($\bar{x}$ = 183 μm; n = 19). Straight hinge larvae were somewhat smaller, ranging from 160 to 190 μm ($\bar{x}$ = 174 μm; n = 10). Newly released juveniles measured at the greatest anterior-posterior distance of their shell were 210–250 μm long ($\bar{x}$ = 236 μm; n = 12). The larvae were not active swimmers. The circular objects and the trochophore-straight hinge stages generally moved little, other than in small circles. The juveniles used their active foot to pull themselves along. However, they did not move very far, tending to remain clumped in the vicinity of the adult which released them rather than spreading throughout the still water of the container.

DISCUSSION

The Asiatic clams sampled in this study were found to be simultaneous hermaphrodites, with male and female reproductive tissue present in all months of the

TABLE II

Monthly values for intercept (u) and slope (v) for allometric equation of log dry tissue weight = u + v log length, with R^2 = coefficient of determination and w = dry tissue weight (mg) of standard Corbicula *sp. of 20 mm shell length*

Month	u	v	R^2	w
1981 Dec	−2.72	3.65	0.988	105.9
1982 Mar	−1.87	2.88	0.954	74.8
May	−1.38	2.83	0.976	199.1
June	−2.13	3.35	0.980	167.9
July	−1.81	3.14	0.968	187.1
Aug	−1.72	3.11	0.982	210.4
Sept	−1.90	3.20	0.973	182.0
Oct	−2.56	3.61	0.973	135.8
Nov	−2.38	3.51	0.982	152.4
Dec	−2.01	3.22	0.979	150.0
1983 Jan	−1.98	3.24	0.992	170.6
Feb	−2.17	3.32	0.986	140.0
Mar	−1.94	3.26	0.994	198.6
May	−1.91	3.18	0.996	167.5
June	−2.10	3.25	0.993	133.4
July	−2.06	3.24	0.993	141.9
Aug	−2.51	3.59	0.994	143.5
Sept	−2.44	3.46	0.987	114.3
Oct	−2.54	3.56	0.968	122.5

year. However, male reproductive tissue was less common than female tissue (Table I, Fig. 2). This has been the case elsewhere, with Heinsohn (1958) being the first to demonstrate this (in California), followed by Kraemer and Lott (1977) in Arkansas and Britton *et al.* (1979) in Texas.

Male and female gametes were found in the smallest clam we sectioned (9.6 mm). Elsewhere, Kraemer (1978) found both types of gametes in Arkansas specimens ≥8 mm long and Aldridge and McMahon (1978) found that Texas specimens were sexually mature at 10 mm. In a summary paper, Britton (1982) gave 7–10 mm as the size at which sexual maturity in *C. fluminea* was attained.

Male tissue represented the smallest tissue VF in the gonadal region (Fig. 2), with highest averages being 6% for developing male gametes and 2% for ripe male gametes. Note, however, that a few clams had extensive development of male tissue, both developing and ripe: Nov. 1982, 21.0 mm; May 1983, 24.5 mm; June 1983, 28.9 mm; Oct. 1983, 30.7 mm (the latter was not included in the sample of 10 clams selected haphazardly for the determination of the VF for October). Again, similar low instances in proportions of male tissue have been reported in Arkansas by Kraemer and Lott (1977) who estimated that male tissue occupied no more than 15% of follicular material, and in Texas by Britton and Morton (1979) who provided an estimate of 30% (in neither case was it explained how the estimates were derived). These low figures are not possible evidence for protandric consecutive hermaphroditism (Britton and Morton, 1979) because the proportion of clams with male gametes increased significantly ($P < 0.001$) with shell size (78% of clams < 20 mm long contained male gametes *vs.* 92% in clams ≥20 mm long) as noted earlier.

The fact that no clear cycles in VF of any reproductive tissue type were demonstrated (Fig. 2) may indicate that Asiatic clams are not much affected by predation and competition (Suchanek, 1978; 1981). It may also indicate that the species is capable of responding rapidly to suitable environmental conditions by spawning at any time of the year. However, the literature contains no evidence that larval production

in the United States has been occurring other than in spring through fall (Heinsohn, 1958; Aldridge and McMahon, 1978; Britton *et al.*, 1979; Eng, 1979; Dreier and Tranquilli, 1981), usually with peak abundances in spring and in fall. [The presence of "larvae" in monthly plankton samples collected over 14 months in the Altamaha River, GA (Sickel, 1979) is not evidence that larval release was occurring monthly. It could be the result of resuspension of juvenile clams by water movement (Prezant and Chalermwat, 1984).] Similarly, at Whites Ferry, clams with larvae in their gills were found over two extended time periods (Table I, Fig. 2). The spring 1982 pulse occurred with water temperatures of 24° to 27°C (we do not know if larvae were present in April 1982 as extremely high river flows and dangerous river conditions precluded collecting material) whereas for spring 1983, the corresponding water temperatures ranged from 17° to 29°C. The fall 1982 and 1983 pulses occurred while temperatures were dropping (from 18° to 2°C in 1982 and 29° to 24°C in 1983). Larvae were found in December 1982 and not in December 1981, perhaps due to the colder temperatures of the latter month (see below). Elsewhere, Aldridge and McMahon (1978) noted that Texas specimens began "spawning" (larval release) at 19°C, with this behavior inhibited by temperatures > 32°C. Fall veliger release declined sharply below 18°C. In California, Eng (1979) found "spawning" (presence of marsupial larvae) to begin as temperatures exceeded 16°C with a second spawning occurring while temperatures were at summer highs.

Percentages of Whites Ferry clams with marsupial larvae (Table I) were greater in spring 1982 (67–85%) than in fall 1982 (10–40%) and in spring 1983 (100% in June) compared with fall 1983 (75–80%). Similar results have been reported for two other populations. In California, Eng (1979) found all clams (100%) sampled in spring 1974 to contain larvae *versus* 20% in fall 1974. In Texas, Aldridge and McMahon (1978) reported 60–90% of adults to be brooding larvae in spring 1975 compared with 20–70% in fall 1975. However, Britton *et al.* (1979) presented a figure for another Texas population (their Fig. 3) showing that whereas in spring of the sampling year approximately 83% of clams contained larvae, in fall a peak of 80% were brooding. Such differences in peak intensity of larval brooding undoubtedly reflect differences in environmental conditions and are probably less important than extent of the brooding and larval release periods. The fall periods when larvae were present were longer than spring periods in Maryland and Texas, but not California (Table I, see also Aldridge and McMahon, 1978; Britton *et al.*, 1979; Eng, 1979). Further, Aldridge and McMahon (1978) quantified larval releases and found a total fall release of over 750,000 veligers m^{-2} compared with spring values of about 390,000 veligers m^{-2}.

At Whites Ferry, a possible response to environmental conditions was noted in the predicted dry tissue weight of a 20 mm animal over the study period (Fig. 3). The collection temperatures for December 1981 and 1982 on Figure 3 can be misleading because, as mentioned, the winter of 1981–1982 was colder than that of 1982–1983. Temperature records made daily in the Potomac River by the Washington Suburban Sanitary Commission reveal that temperature from December 1981 to February 1982 ranged from 1.0 to 3.3°C with minima of 0.0 to 1.0°C and maxima of 1.4 to 7.0°C. Temperatures increased from December through February. By contrast, from December 1982 to February 1983, average temperatures were 4.6–8.7°C, with minima of 1.0–5.0°C and maxima of 7.0–15°C (temperatures decreased from December to February). These temperature differences may account for the different predicted dry body weights for the two collection periods (Fig. 3), with weights in December 1981 and March 1982 being up to 60% lower than for comparable periods in 1982–1983. On the other hand, dry weights increased rapidly in early 1982 after the cold winter, reaching levels greater than in comparable months in 1983. Although the colder winter may have depressed body weights until spring, the population which

survived the winter recovered body weight quickly and produced larvae over four different time periods thereafter until our sampling ceased (Fig. 2). Indeed, in September 1983 we estimated clam densities to exceed 10,000 m^{-2} at Whites Ferry. This recovery from a very cold winter is significant because Asiatic clams are considered to be intolerant of severe winter conditions, thus being generally limited to areas below 40° N latitude (Britton and Morton, 1982). They may be able to escape the cold by burrowing more deeply into the sediment. Our subjective impression is that they lie nearer the surface of the river bed in summer (where they are readily seen) than in winter (when they are much less conspicuous, even in the clear water of that time of year).

In conclusion, Asiatic clams from this more northerly population were broadly similar in their reproductive patterns to those populations that have been studied further south in the United States. Given the year-round presence of eggs and sperm and their occurrence in clams from about 10 mm in size and up, the brooding of larvae for two relatively long periods per year, and the possibility of self-fertilization, it is probable that the recent invasion of this exotic species into Maryland waters will continue and expand.

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